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Author(s): Kendi F. Davies, Chris R. Margules, John F. Lawrence

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A SYNERGISTIC EFFECT PUTS RARE, SPECIALIZED SPECIES AT GREATER RISK OF EXTINCTION

KENDI F. DAVIES,^{1,4} CHRIS R. MARGULES,² AND JOHN F. LAWRENCE³

¹*Division of Botany and Zoology, The Australian National University, Canberra ACT 0200, Australia*

²*CSIRO Sustainable Ecosystems and Tropical Forest Research Centre, P.O. Box 780, Atherton QLD 4883, Australia*

³*CSIRO Entomology, Box 1700, Canberra ACT 2601, Australia*

Abstract. Theory and empirical evidence have long suggested that some species are extremely vulnerable to extinction because they have combinations of extinction promoting traits. However, ecologists have not considered whether the form of the relationship between traits is additive (not synergistic) or nonadditive (synergistic). We looked at how traits and their interactions were related to the difference in species' population growth rates between experimentally fragmented forest and continuous forest. Two traits acted synergistically; natural abundance and degree of specialization interacted so that beetle species that were rare and specialized had a greater reduction in their growth rates in fragments, compared to continuous forest, than the sum of the reductions in growth rates attributable to these traits. In other words, species that were both rare and specialized were especially vulnerable to extinction. From a conservation perspective, an implication of our findings is that making predictions about extinction risk from a single trait, like abundance or population variability, may be risky because traits may act synergistically rendering species more, or less, vulnerable than predicted by that single trait. There is currently a great deal of interest in which traits predict the sensitivity of species to a given threat, but if we are going to look at risks in this way, then we also need to consider how traits interact, because this can alter the vulnerability of species.

Key words: beetles; biodiversity; body size; extinction risk; forest; fragmentation; habitat specialization; matrix; population dynamics; rarity; trophic group.

INTRODUCTION

Theory and empirical evidence suggest that some species are extremely vulnerable to extinction because they have combinations of traits that promote extinction. It has long been known that life-history traits are related to the dynamics of populations, including colonization ability and extinction risk, which means that traits may act as surrogates for extinction risk when we lack better data (Cole 1954, Elton 1958, MacArthur and Wilson 1967, and see McKinney 1997, Fagan et al. 2001). Examples of such traits include rarity (Simberloff 1986, Pimm 1991, Caughley 1994, Lawton 1994), degree of habitat specialization (Frank and Amarasekare 1998), trophic level (Pimm and Lawton 1977, Holt et al. 1999), and body size (Lawton 1994, Blackburn and Gaston 1997). Empirical evidence supports these predictions. Species' declines and extinctions have been correlated with rarity (Robinson and Quinn 1988, Duncan and Young 2000, Davies et al. 2000, 2001b), habitat specialization (Foufopoulos and Ives 1999, Owens and Bennett 2000), trophic group (Lawler 1993, Holyoak 2000, Davies et al. 2001b), and body size (Burbidge and McKenzie 1989, Gaston and

Blackburn 1995, Owens and Bennett 2000). In addition, in combination, these traits further increase a species risk of extinction (Lawton 1994).

So far, however, there has been no consideration of how traits combine to increase extinction risk: Are the effects of traits in combination additive or nonadditive? For example, in reviews of traits that make species extinction prone, both Lawton (1994) and McKinney (1997) use the term "synergistic combination" for the traits of rarity and specialization. They argue that since rarity is often associated with being specialized, specialized species may be prone to multiple risks produced by a combination of fewer individuals with a narrower tolerance to change. But these authors did not distinguish whether synergism implied additivity or nonadditivity of effects. Similarly, fossil evidence suggests that extinction-promoting traits like rarity and being specialized may co-vary (Lawton 1994, Brown 1995) because both background and mass extinctions show nonrandom taxonomic patterns. That is, some phylogenetic groups are better represented than others (Jablonski 2001). But knowing that traits covary does not tell us how the effects of those traits act together to promote or reduce extinction risk. Thus, when we speak of synergistic combinations of traits and of covariance between traits, there is ambiguity about the form of the relationship between traits, which needs to be clarified.

Here, we constructed a test for synergistic effects using a multiple regression analysis that tests for the

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⁴ Present address: Department of Environmental Science and Policy and Center for Population Biology, University of California, Davis, California 95616.
E-mail: kfdavies@ucdavis.edu

significance of interactions between traits of beetle species (rarity before fragmentation, degree of habitat specialization, trophic level, body size) and the effects of experimental habitat fragmentation. In multiple regression, interactions measure nonadditivity. We look at how traits and their interactions were related to the difference in species' population growth rates between experimentally fragmented forest and continuous forest. We hypothesized that we would find nonadditive relationships between at least some of the four traits considered, given the prevalence of the idea of synergistic interactions in the literature. Here we assumed that a declining growth rate in fragments compared to controls equates with increased extinction risk. Whether species with declining growth rates are headed toward extinction is uncertain, and does not necessarily follow from theory. However, large populations typically become small populations before going extinct (Hanski et al. 1994).

METHODS

Experimental design

The Wog Wog habitat fragmentation experiment is located in southeastern New South Wales, Australia (37°04'30" S, 149°28'00" E; Fig. 1) in native *Eucalyptus* forest. The experimental design and the rationale for it were described by Margules (1993). Briefly, it consisted of three plot sizes: 0.25 ha, 0.875 ha, and 3.062 ha. Four replicates of each size (12 plots) became habitat fragments when the surrounding *Eucalyptus* forest was cleared in 1987 and planted to *Pinus radiata* for plantation timber. Two replicates of each size (6 plots) remained in uncleared continuous forest, and served as the unfragmented control plots. Within each plot or fragment, there are 8 monitoring sites, giving a total of 144 sites. Two permanent pitfall traps were located at each monitoring site. Traps were opened for 7 d four times a year, once during each season.

Monitoring commenced in February 1985, and two years of data were collected prior to the fragmentation treatment for all plots. The experimental treatment, habitat fragmentation, took place over 9 mo in 1987. The pine plantation was established in winter 1988, and an additional 44 monitoring sites were established in the *P. radiata* plantation between the habitat fragments.

A total of 655 beetle species had been captured by winter 1992. Half of these species have not yet been named, although all species have a voucher number. Roughly three-quarters of species were captured fewer than 10 times. More than one-third (263) of species were captured only once or twice. These incidental captures may represent species that are either rare, are not habitually ground dwelling, or that move little and are therefore unlikely to fall into pitfall traps. Although it would be interesting to know the effect of habitat fragmentation on these species, there is little that we can

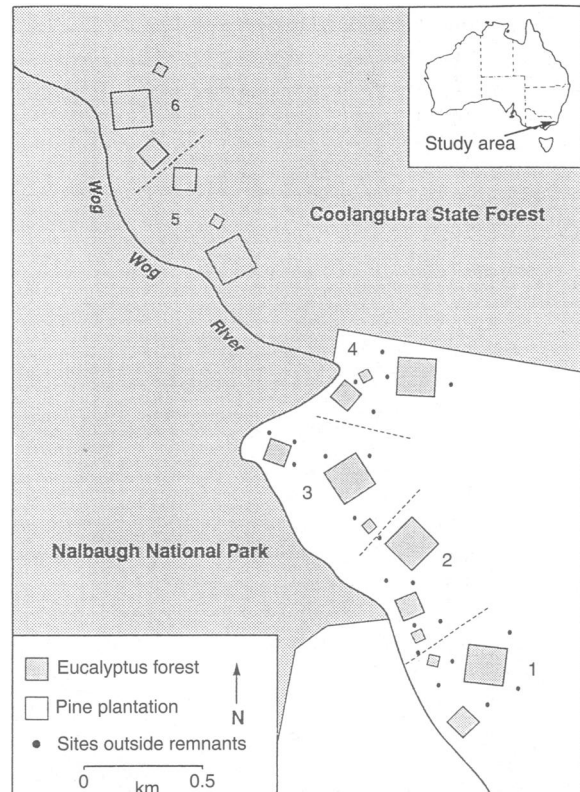


FIG. 1. Map of the experimental site showing eucalypt forest fragments and control plots in continuous forest. Dots represent the location of a pair of monitoring sites (a slope site and a drainage line site) established in the pine matrix between the remnants after fragmentation. There were eight monitoring sites within each fragment where pitfall traps were opened in each season for two years before fragmentation and for five years after fragmentation (fragment sizes: 0.25 ha, 0.875 ha, and 3.062 ha). Fragments were separated by at least 50 m.

infer from so few captures. We studied species that had been trapped at least 23 times after the fragmentation treatment was applied because the standard error of the response metric rose markedly for species that occurred fewer than 23 times. Below this, the standard error for many species was larger than the response metric. From a total of 655 species trapped, this gave us 71 study species from 16 families.

Data analysis

There were two steps to the analysis. First, we analyzed the response of each species to fragmentation using Poisson regression and formed a response metric using the estimates from these analyses. Second, these response metrics (one for each species) were then used as the dependent variable in a multiple regression analysis with species' traits as the independent variables. To examine synergistic effects of traits, we tested for interactions between traits in the multiple regression analysis. We used Genstat 5, release 4.21, for all analyses (Genstat 5 Committee 2000).

Calculating the response metric.—We analyzed the response of each of the 71 species to habitat fragmentation using Poisson regression. We used this statistical modeling approach to calculate a response metric because it best dealt with the discrete nature of our data, allowed us to incorporate the spatial structure of our experimental design, and provided appropriate estimates for the standard error of the metric. Our data consisted of counts of the number of individuals caught per trapping site. Since the numbers caught were small, it was important to account for the discrete nature of the data. Thus, we used Poisson regression, specified as a generalized linear model with log link function and Poisson likelihood (McCullagh and Nelder 1989). The analysis is described in detail in Davies and Margules (1998, see also Davies et al. 2000). Here we give a brief description.

To determine the response of each species to habitat fragmentation, we analyzed the number of individuals caught at each of the 144 sites totaled over years three through five, post-fragmentation. For nearly all species, there were not enough data to treat years or seasons separately. For the very abundant species, for which we could have considered years separately, visual inspections of the data suggested that the summed responses were representative of the responses of species with years considered separately. Data from the two years immediately after fragmentation were not included because the disturbances that occurred during that period (clearing, burning, and planting of *P. radiata*) may have been confounding. Captures from the two years before fragmentation were included in the model as a covariate, the natural logarithm of abundance before fragmentation. This covariable acted to remove any effect of uneven spatial distribution in abundance before fragmentation. To account for the nested spatial structure of the experimental design (sites nested within fragments within replicates), we included additional terms in the model to remove these random effects (described in detail in Davies and Margules 1998). We did not consider patch size. For each of the 71 species, we used the statistical model to estimate the mean number caught per trapping site in fragments and continuous forest controls, after fragmentation, adjusted for differences in initial abundance.

We estimated the response to fragmentation as the log ratio of beetles in the fragments and continuous forest:

$$\text{response} = \ln(N_{\text{fragments}}) - \ln(N_{\text{controls}}) = \ln\left(\frac{N_{\text{fragments}}}{N_{\text{controls}}}\right) \quad (1)$$

where N is the mean number of beetles caught per trapping site after fragmentation. In practice, we obtained the difference $\ln(N_{\text{fragments}}) - \ln(N_{\text{controls}})$ and the standard error of the difference directly from the sta-

tistical model with no back transformation, since the difference is expressed on the scale of the linear predictor in the generalized linear model (McCullagh and Nelder 1989). Subsequently, we used the response ratio in Eq. 1 as our metric of a species' response to fragmentation.

An important property of the response metric in Eq. 1 is that we can derive a biological interpretation (Osenberg et al. 1999). The theory that we tested makes predictions about traits of species in relation to their probability of extinction, so our attention is focused on changes in beetle population dynamics in fragments compared to continuous forest. The response metric in Eq. 1 can be interpreted as measuring the change in population growth rate due to fragmentation, since

$$r_{\text{fragments}} - r_{\text{controls}} = \ln\left(\frac{N_{\text{fragments,final}}}{N_{\text{fragments,initial}}}\right) - \ln\left(\frac{N_{\text{controls,final}}}{N_{\text{controls,initial}}}\right) \quad (2)$$

where N_{final} is abundance after fragmentation, N_{initial} is abundance before fragmentation, and r is the time-averaged growth rate for the discrete interval from before to after fragmentation. For the same N_{initial} in fragments and controls, Eq. 2 reduces to Eq. 1. It is reasonable to assume that initial abundance does not differ systematically between fragments and controls, since initial abundance is a random variable (the fragmentation treatment was not applied until after initial abundance was measured) and by including $\ln(N_{\text{initial}})$ as a covariate in the model for individual species, the final abundance was adjusted appropriately. Hence, the response metric can be interpreted as a measure of the change in the growth rate of populations in fragments compared to controls, that is, the change in the growth rate that is caused by fragmentation.

The metric in Eq. 1 also has several statistical advantages (Hedges et al. 1999). First, the response is proportional rather than absolute. This was important because the range of beetle abundances post-fragmentation was large (23–11 443). Second, the natural logarithm linearizes the metric, so changes in the numerator and denominator are treated equally. Third, the distribution of the logged response ratio is approximately normal.

Because we restricted the analyses to species that had been captured at least 23 times post-fragmentation, we did consider that our pool of subject species might be biased toward species that became common subsequently, regardless of their initial abundance. However, this does not bias the analysis because the contrast that we made is between species growth rates in the continuous forest controls and growth rates in fragment treatments. That is, we formed the response ratio using the *after* fragmentation data. We simply left out all those cases where the species was so rare in *both* fragments and controls *after* fragmentation, that the re-

sponse ratios formed for the analysis would be unreliable. There is no bias because species that were previously rare, and remained in the analysis, *could remain rare* in one or other of fragments or controls, while becoming more common in the other treatment. Since species that were previously common could do the same, there is no bias.

Species responses and combinations of traits.—Four species traits were considered. (1) Natural abundance: For each species, we summed catches for the two years of sampling that took place before the fragmentation treatment was applied. (2) Habitat specialist/generalist: We considered whether a species was ever caught in the pine matrix in five years post-fragmentation. We considered those beetle species that were never trapped in the pine matrix to be specialists, and those species that were trapped in the pine matrix to be generalists. *P. radiata* is not native to Australia. When grown as a plantation timber, it forms stands with little or no herbaceous layer or understorey, and the forest floor litter is much simpler in structure than in the native eucalypt forest it replaces. Species that were trapped in the matrix either were able to colonize this habitat, which was alien to them, or were able to disperse through the matrix between fragments. Thus, we are confident that if a species was never caught in the pines, it was indeed a specialist of eucalypt habitat. Conversely, it is possible that some species caught in the pines were actually specialists of eucalypt forest and were only dispersing through the pines rather than living there. Therefore, it is most accurate to describe species that were never caught in the pines as specialists that were isolated on habitat fragments (Davies et al. 2000). However, the degree of misclassification of specialists as generalists is likely to be very low. For example, in mark-recapture studies of three of the largest species, we have recorded mean dispersal distances of 5–10 m and a maximum distance of 25 m (K. F. Davies, *unpublished data*). Despite low dispersal ability, these species were caught frequently in the pines (ratio of captures in pines vs. eucalypts of 0.5–1.7), suggesting that they were indeed generalists with populations established in the matrix and were not merely dispersing into it. (3) Body size: With micro callipers, we measured total beetle body length, and breadth across the widest part of the body, in millimeters, to the nearest 50 microns. We then multiplied these measures to provide a measure of body size, which was logged for the regression analysis. (4) Trophic group: Beetles were assigned to one of three trophic groups: (1) species feeding on dead wood and detritus, (2) herbivores, and (3) predators. Most assignments were made at the genus or subfamily level.

We used multiple regression to test for the combined effects of these four traits on beetle responses to fragmentation and to test whether the effects of traits in combination were additive or synergistic. To test whether the effects of combinations of traits were ad-

ditive or synergistic, we considered traits both on their own and as interactions. A significant interaction term would indicate a synergistic effect of traits in combination, whereas a lack of significant interaction terms would mean that the effect of traits in combination was additive. Model fitting took place as follows. First, the full model was fitted, which included the four traits and all possible first order interactions. For each term we conducted a conditional test of significance by dropping it from the fullest possible model. Values of P were calculated from variance ratios, and a variable was considered significant when $P < 0.05$. Thus, the effect of each trait (main effects and interactions) on the response metric was considered after the effects of all other traits had been accounted for. To check for collinearity, we tested for correlations between the trait variables using simple linear regression. None of the variables were significantly correlated with one another. As an additional check on collinearity, we conducted marginal tests (adding terms to the minimal possible model) and found that, although variance ratios changed very slightly, the identity of significant terms did not change from the conditional tests, thus indicating lack of collinearity since the test results were not sensitive to the order in which terms were added to the model. Significant variables were included in the final model. Departures of the data from the model assumptions were determined by viewing histograms of the data, plots of residuals vs. fitted values, and plotting residuals as a normal order probability plot. One outlier was removed, improving the fit of the final model. The natural abundance of generalist species had a range that was 50 times greater than that of specialist species. Log-transforming natural abundance did not satisfactorily address this problem, so we further restricted our data set so that the ranges in abundance for both groups were the same (1–50). This ensured that any significant interaction terms were not merely due to different ranges in the independent variables. This gave 55 species to be considered in the trait regression analysis. To compare with analyses on the reduced dataset, we also fitted regression models for the full dataset of 71 species. However, four species with natural abundance >20 times higher than other species consistently had undue leverage on the linear regression and made linear assumptions untenable for these models. When these species were excluded, the results were similar to the analysis of 55 species.

Finally, it may appear that, by not including those species that occurred <23 times, we were throwing out a lot of data and discarding the signal of the rarer species. We argue that it makes little sense to try to say anything about a species that occurred only a handful of times in seven years of trapping and that including these species would have contributed noise to our findings. However, these species were included in a community level analysis in another paper (Davies et al. 2001b), the results of which are consistent with

TABLE 1. Full and final models from multiple regression analysis of beetle responses to experimental fragmentation as a function of traits of species.

Source	df	MS	F	P
Full model				
Natural abundance	1	0.41	0.45	0.51
ln(body size)	1	0.00	0.00	0.97
Specialist/generalist	1	13.01	14.13	<0.001
Trophic group	2	1.82	1.98	0.15
Natural abundance \times ln(body size)	1	0.30	0.33	0.57
Natural abundance \times specialist/generalist	1	4.07	4.42	0.04
ln(body size) \times specialist/generalist	1	0.13	0.14	0.71
Natural abundance \times trophic group	2	0.61	0.67	0.52
ln(body size) \times trophic group	2	0.57	0.62	0.54
Specialist/generalist \times trophic group	2	0.46	0.50	0.61
Error	39	0.92		
Total	53			
Final model				
Natural abundance	1	0.41	0.49	0.49
Specialist/generalist	1	12.83	15.08	<0.001
Natural abundance \times specialist/generalist	1	4.99	5.87	0.02
Error	50	0.85		
Total	53	1.15		

Notes: One outlier was removed. Values of *P* are for conditional tests.

those presented here, although we were not able to consider interactions between traits in that paper.

RESULTS

There was a significant interaction between a species' natural abundance and level of habitat specialization (Table 1), so that the growth rate of rare species that were habitat specialists declined significantly more in fragments compared to continuous forest than the

additive effects of natural abundance and habitat specialization accounted for (Fig. 2). Habitat specialists that were not also rare did not decline. In contrast, the natural abundance of a species did not matter if it was a habitat generalist. For example, rare generalists fared about the same as abundant generalists. In fact, our final model predicted that the growth rate of all generalist species increased slightly in fragments compared to continuous forest, following fragmentation, regardless of whether they were rare or abundant (Fig. 2). The final model accounted for 25.8% of the variance (measured as adjusted R^2 ; Genstat 5 Committee 2000). In contrast, an additive model with both natural abundance and habitat specialist/generalist as main effects, but no interaction accounted for 18.7% of the variance. Thus, including the interaction improved the amount of variance explained by more than one-third over the additive model. The difference in the slope of change in growth rate vs. natural abundance between specialists and generalists was 0.054 in the nonadditive model. In contrast, the joint slope in the additive model was 0.006. Thus, the difference in the slope was nine times greater than the joint slope, and is one measure of the biological significance of the interaction.

Of the four traits and their first order interactions that we tested, only natural abundance and the interaction between natural abundance and habitat specialist/generalist were significantly related to the responses of beetle species to habitat fragmentation (Table 1). To reassure ourselves that the significance (or lack of significance) of the continuous variables body size and natural abundance, and all interactions with these variables, were not sensitive to data transformations, we tested all possible combinations of the model that included logged and unlogged versions of these variables. The same terms were significant in all models.

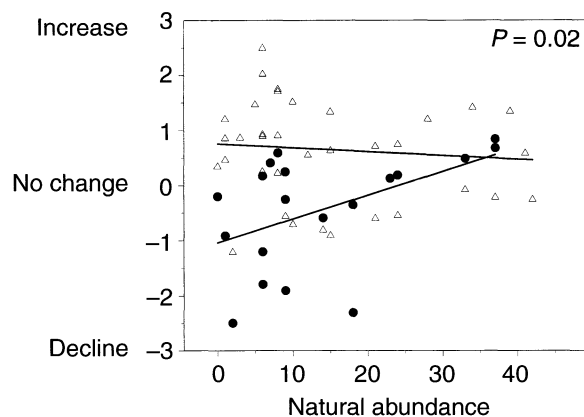
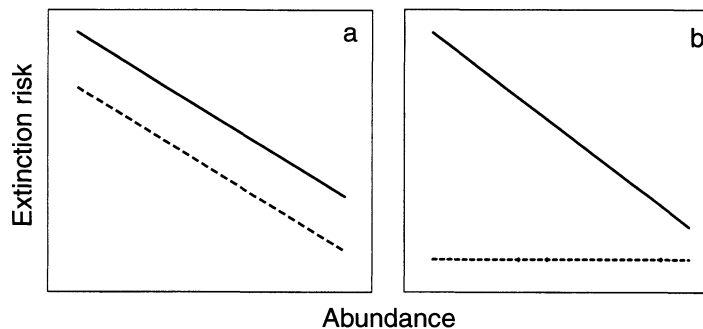


FIG. 2. Nonadditive model of the responses of beetle species to fragmentation based on their natural abundance and whether they were habitat specialists or generalists. The x-axis represents the change in the growth rate of a species in fragments compared to continuous forest, after fragmentation. Points below zero represent a reduction in average growth rate as the result of fragmentation. A decline of "1" in growth rate represents a threefold decrease in abundance in fragments compared to controls ("–2" represents roughly a seven-fold decrease). Natural abundance was measured over two years before the fragmentation treatment was applied. The lines represent predictions from the regression model. Circles are habitat specialists, and triangles are habitat generalists.

FIG. 3. Schematic contrasting (a) additive and (b) synergistic relationships between degree of specialization and natural abundance. In (a), there is no interaction between degree of specialization and natural abundance, and thus the lines are parallel. In (b), there is an interaction between degree of specialization and natural abundance; thus the lines are not parallel, and a synergistic effect is implied. Solid lines are habitat specialists, and dashed lines are habitat generalists.



DISCUSSION

Two traits acted synergistically to determine the effect of habitat fragmentation on beetle species. Abundance and specialization interacted so that rare and specialized species had a greater reduction in their growth rates than the sum of the reductions in growth rates attributable to these traits (Fig. 2, Table 1). In other words, species that were rare and specialized were especially vulnerable because they have a synergistic combination of extinction promoting traits (Lawton 1994, McKinney 1997). Although unlikely, it is possible that some specialists were misclassified as generalists (but not vice versa). Then, the above result applies strictly to isolated specialists. In contrast to specialists, rare generalists fared about the same as abundant generalists. In fact, the growth rate of generalist species increased slightly in fragments compared to continuous forest, regardless of whether they were rare or abundant. Our result provides evidence that synergistic interactions between traits can put species at greater risk of extinction than the additive effects predicted by single traits.

These findings illustrate that it is important to make the distinction between whether traits act additively or synergistically, because this can dramatically affect probability of extinction in fragmented landscapes. For example, for beetle species, if the effects of degree of specialization and natural abundance had been additive, then we would predict that the growth rate of rare generalists would also have been reduced in fragments compared to continuous forest and the growth rate of rare specialists would be reduced much less than we observed (Fig. 3a).

Interestingly, one of the most basic predictions of metapopulation theory is that the effects of specialization (or isolation) and rarity are synergistic in the way we find here (Hanski et al. 1994). This is interesting, because although ideas about the form of the relationship between traits have not explicitly been explored theoretically, they actually follow naturally from current theory, at least for rarity and degree of habitat specialization for fragmented landscapes. This synergistic effect is most clearly seen in the extreme case, in which we contrast a species that is completely isolated with a species that is not isolated at all (corre-

sponding to a highly specialized and highly generalized species). If a species is not isolated, then there is no additional effect of rarity when the landscape is fragmented. When a species is isolated, the effect of fragmentation on it is much larger when it is also at low abundance than when it is at high abundance (Fig. 3b). Thus, this well-known result is a synergistic effect of isolation and rarity. One may argue that this extreme case is not very interesting, since if a species is not fragmented into isolated populations, then there can be no effect of fragmentation. However, the extreme case marks the bounds of intermediate situations, for example, in contrasting species that are partially isolated. These intermediate cases, which are likely the most common, retain the synergistic effect.

Empirically, there is plenty of evidence that rarity and habitat specialization, in particular, are traits that place species at risk. For example, extinction rates were highest in rare, specialized lizards and snakes on Greek islands (Foufopoulos and Ives 1999), but a nonadditive relationship between abundance and degree of specialization was not tested for. Plant species that were rare about the time that settlers begun to clear land around Auckland, New Zealand, were much more likely to be extinct in 1985 than species that were initially common (Duncan and Young 2000). Habitat loss threatened bird families that were specialists more than families that were not (Owens and Bennet 2000). Finnish dragonfly species that were habitat specialists were more extinction prone than generalists, probably because they also tended to be rare (Korkeamaki and Suhonen 2002). Finally, the only trait that distinguished rare from common primate taxa was degree of specialization, and not high resource requirements or slow population recovery rate (Harcourt et al. 2002).

From a conservation perspective, an important implication of our findings is that making predictions about extinction risk from a single trait, such as abundance or population variability, may be risky because traits may act synergistically, rendering species more, or less, vulnerable than predicted by that single trait. Generalists do tend to be widespread and abundant (Lawton 1994), but what happens to those species that are not? Similarly, specialists do tend to be rare, but when they are not, how does their risk of extinction

change? When linking extinction risk and traits, we need to explore these kinds of questions.

In summary, we found that synergistic effects of traits can significantly increase the sensitivity to habitat fragmentation of rare, specialized species. There is currently a great deal of interest in which traits predict the sensitivity of species to a given threat, such as habitat fragmentation (e.g., Didham et al. 1998, Davies et al. 2000, 2001a, b, Steffan-Dewenter and Tscharrntke 2000, Fagan et al. 2001). But if we are going to look at risks in this way, then we also need to consider how traits interact, because interactions can alter the vulnerability of species.

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